

CERTAIN PROBLEMS OF PALEOZOOGEOGRAPHY

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The dismembered skeletons of vertebrates yield a complete concept of their organisms and permit the functional significance of individual features and the general structure and biology of the animal to be fully restored. The mammals studied by Vladimir Kovalevskij and many other paleontologists have provided a broad basis for paleoecological and phylogenetic conclusions.

The mammals abundantly and diversely represented by present fauna supply the richest material for comprehending and restoring extinct groups. Due to the fact that mammals are in most cases strictly confined to certain narrow conditions, they are extremely important in revealing the landscapes of the past. The vast variety of biological types among mammals and the equally great number of ecological niches which they occupy make them excellent landscape indicators. The close relationship existing between herbivorous mammals and flora provides an even surer basis for judging the conditions under which one species or another lived. It must not be forgotten that the slightest deviations in the nature of the vegetation consumed by mammals and the manner in which this vegetation was obtained are mirrored sharply in the mammals' structures.

It is very likely that all of the foregoing makes mammals, as compared with other terrestrial vertebrates, one of the best means by which continents may be paleogeographically reconstructed. There are several groups of insects which are also good landscape indicators, but insects are comparatively rarely preserved in sufficient entirety and their locations are more sporadic. Insects, therefore, cannot yield as complete a picture as mammals.

The extensive studies undertaken by Soviet paleozoologists on the continental faunas of the Soviet Union and Central Asia have contributed greatly to the knowledge of the past. Even more immense unsolved problems, however, remain before us. An enormous gap in our knowledge is the complete absence in the USSR of mammals from the Mesozoic, which have been found in western Europe and America. Furthermore, not to mention the fact that we are still a long way from a detailed clarification of the composition and phylogeny of various groups of vertebrates which once populated the USSR, we know very little of the ecology of the forms which have been found and, particularly, of their geographic distribution. Our knowledge of the formation of and changes in faunistic complexes and their distribution,

ties and interrelations with the complexes of other countries, is very meager.

It may be stated, incidently, that the term "cenogenesis", introduced by V.N. Sukachev in 1944 and 1958, is not entirely felicitous, although it expresses well the notion of the development of associations in the course of geological time, bringing in the biocenological concept of the processes of the historical development of organic groupings and clearly defining the phenomena of unity and interaction in time of biological associations among themselves and with the surrounding physical medium. But since it was first employed by E. Haeckel in his book Anthropogenie in 1903 to designate the embryonic and larval adaptations of animals in relation to their environment, and was subsequently used in this sense, it would be better to replace it with another.

In 1962, O. Reig, developing Sukachev's ideas, proposed the use of the terms "zoocenogenesis" and "phytocenogenesis" for cases in which phenomena of the animal and plant worlds were being examined individually. Reig was later quite correct in deeming it necessary to replace the concept of the "faunistic layer", introduced by D. Simpson in 1950 to designate groups or associations of animals inhabiting a certain area at a certain moment of geological time, by the term "cenochron". Reig clarified and expanded this concept as follows: "The cenochron is a group or association of animals or plants of varying origin intruding upon a definite geographical range in the course of a definite space of geological time" (Reig, 1962, p. 133).

It must be admitted that problems of cenology, of the development of associations and of many other divisions have been better elaborated in geobotany than in zoogeography. It is very likely that the same applies to corresponding departments of paleobiogeography. The problems of paleozoogeography and their interrelations with zoogeography have hitherto not been properly established.

How, then, may these disciplines now be conceived? Should they be considered as a single whole or must they be divided into two independent sciences, each confronted with its own special problems? We shall attempt to determine the basic problems of both divisions.

Zoogeography is a department of biogeography which studies the present distribution of animals, the history of their origin, the formation of the present complexes existing in the animal world, and the factors and laws determining animal distribution. These extremely broad problems can be solved only by using information from many sciences. The investigation of the geographical distribution of the animals which we now observe on the earth requires not only zoological and botanical studies but, to no less a degree, information supplied by geomorphology, climatology and geology as well.

The range of the problems which paleozoogeography is called upon to solve is even broader and more complex than that confronting zoogeography both because of the incompleteness of the geological chronicle and because

of the methods used in the research itself. Zoogeography enables us to observe directly the present geographical ranges of animals; our paleontological information on past geological ages is, however, very meager at all times. Zoogeography is concerned mainly with a very short segment of time, from the geological point of view, and, with rare exceptions, employs mainly paleontological data from the most recent stages of geological history to investigate problems arising from the present distribution of animal groupings. The problems of paleozoogeography are different. Paleozoogeography is a field of biogeography which studies the history of the distribution of the animal world of the past, the successive origin, change and distribution of faunistic complexes, cenochrons, the ways in which the latter were formed in various geological periods, and their evolution, settlement, intercontinental migrations, formation and extinction; paleozoogeography is the science which studies the causes and laws governing these processes.

In no case must paleozoogeography be confused with "historical zoogeography", a synonym for the so-called historical trend of causal zoogeography, i.e., the division of zoogeography which investigates the dependence of the present distribution of animals upon events occurring in the past. Paleobiogeography is a very suitable term for defining a certain discipline. It is therefore difficult to agree with Reig's proposal of 1962 that the term "cenogenesis" be substituted for the whole of historical biogeography on the grounds that all modern scientific biological investigation proceeds from the theory of evolution. There can, of course, be no basis other than evolutionary in modern science, but this is hardly involved in the naming of a science.

Thus both divisions of biogeography, which are doubtless related in the closest way, have nonetheless entirely independent problems, methods and ties with other branches of science. Zoogeography is mainly related to the zoological disciplines - ecology and taxonomy; it is of very great importance in the study of theoretical problems of taxonomy, and so on. Zoogeographical data are of less significance in paleogeography and, as noted above, are of value chiefly for the most recent times. Paleozoogeography yields vast material for the study of problems of species formation, morphology, and evolution and represents one of the most important means of studying paleogeography and the landscapes of the past, thereby serving practical geology.

It is quite clear that the methods used in conducting paleozoogeographical investigations differ considerably from the methods of zoogeography.

As stated above, we are unable to ascertain with accuracy the regions inhabited in the past by separate species or species complexes forming natural associations and definite groupings peculiar to various geographical districts, landscapes or climatic zones. In other words, as far as the past is concerned, we have no full concept of geographical range. In studying the past stages of the development of animals we come up against numerous, disconnected locations of individual animals and whole "faunas", i.e. groups of animals buried together; we can never, however, establish the entire region inhabited by a given species.

The paleontologist must first of all ascertain the nature of the burial; he must then investigate the morphological and taxonomic position and adaptations of components, size up their biological types and ecology, and indicate, as far as possible, by comparing locations of the same age (which is always difficult to establish) at various geological points, the territory occupied by individual species and complexes. Morpho-ecological analysis will assist in obtaining a fairly clear idea of the nature of adaptations, mode of life and habitat. Comparing botanical, paleoclimatic and physiogeographical data, the paleontologist examines individual ecological and geographical groupings and complexes for each segment of geological time and traces both their geographical distribution and their change in the course of time. Both the horizontal and chronological distribution of these groupings and complexes as well as their changes are retraced against the background of physiogeographical conditions.

Available fragmentary data (for disconnected locations) on distribution are combined on the basis of information obtained as to the ecological affiliation of separate species, groupings and complexes. Their affiliation with a given landscape may occasionally enable geographical ranges to be ascertained within, of course, only very approximate limits. Both physiogeographical and paleobotanical data, therefore, must serve as the foundation for research of this type. Such a many-sided systematic means of study will permit a relationship to be established among individual, frequently far-flung points where discoveries have been made and a more or less harmonious picture of distribution to be developed. Under no circumstances, however, can the distribution of animal species be mechanically "adjusted" on the basis of their ecological peculiarities with respect to botanical landscape zones. Such adjusting can lead to extremely "broad", but wholly incorrect generalizations.

Landscape must be considered as one of the most important factors in the distribution of mammals. Special, fairly well adapted complexes are now and have been peculiar to various landscape zones. It must first of all be understood that the basic types of landscape currently existing on the earth are by no means fully representative of those which existed in the past. Many of to-day's biotopes were, in the past, completely differently distributed. Thus, for example, the area of subtropical fringing river valley forests, separated by elevations with thinned forest-steppe vegetation and presently covering a comparatively limited area in south-eastern Asia embraced, in the Oligocene, a broad strip extending for a vast distance throughout the entire temperate and subtropical region of Asia and Eastern Europe.

Furthermore, it is a known fact that areas once adjacent to huge estuaries which periodically flooded vast tracts of surrounding forest, similar to the Amazon gapos, were located in many areas on other continents as well. In addition, there existed completely distinctive, peculiar types of biotopes which are absent from present landscape zones. The paleo-zoogeographer, therefore, must investigate the types of terrestrial biotopes individually for each segment of time and explain their nature and successive changes in order to discover the causes and patterns of change in the animal population.

Hence in studying the paleozoogeography of mammals, we can give only the most general outline of landscape groupings; nonetheless the main dependencies of mammal distribution upon the nature of the landscape can be perceived.

The basic landscape units of both the present and the past are forest, open steppe and desert, circumpolar arctic regions, alpine highlands, and, finally, swampy regions and those adjacent to water areas. But, we repeat, both the nature and the distribution of these units have been subjected to tremendous changes in the course of geological history. Because of this, both the nature of all fauna and the aspect of its individual representatives have altered sharply. Thus in the Paleocene and the Eocene we find abundant remains of mammals, forest and swamp dwellers whose existence was contingent upon a warm, fairly moist climate and widely distributed damp forests, swampy tracts adjacent to numerous water areas, and very limited open landscapes. Animals adapted for life in dry, open areas were practically non-existent.

The drying process which began with the Eocene and was more clearly evident in the Oligocene involved the emergence of territories with thinned stands of timber; at the same time, an abundance of mammals clearly adapted to dry areas with hard soils was characteristic of the early and middle Oligocene. An example of this may be seen in the Indricotherium fauna of Kazakhstan (Flerov, 1961).

Frequent mention is made of the movement of an entire complex or fauna from a certain region or place of origin. Here, however, it must primarily be borne in mind that an entire fauna does not move as a single unit; rather, individual components move and various species migrate in various ways. Such migrations can be swift or slow; gradually a whole complex is displaced, covering a wide area in the process. Such cases, however, are very rare; ordinarily, different species migrate at different speeds and various obstacles exist for various species. Thus, for example, when Hipparion fauna migrated from Asia, where this complex had been formed, to Africa, some of the species did not penetrate the steppes: deer characteristic of Asiatic Hipparion fauna are completely non-existent in Africa. Similar examples could be quoted.

It must be stressed that there is a considerable difference between the movement of certain populations of organisms within a given space and the processes by which geographical ranges change. Thus the term "migration" is applied to the seasonal roaming of northern deer and other hoofed animals and to similar movements of lemmings, squirrels, etc. At the same time the term "migration" is also ordinarily used for expressing a shift in geographical range, its movement, expansion, etc.; hence this latter idea is more conveniently expressed by the concept of "prochoresis", established by H. and J. Termier in 1956.

When we speak of the prochoreses of whole faunas, we must first of all stress the basic importance of a knowledge of the ways, trends, and speeds of migration. In investigating ways and trends, we at the same time investigate the obstacles to the settlement both of an entire fauna and of

its individual components; these obstacles depend to a considerable extent upon geological transformations. The rate of speed at which an entire complex and its constituent individual species move, should next be investigated. Of course, when intercontinental links originated between Asia and America through the formation of land in what is now the Bering Strait, various species crossed at various speeds and likewise overcame obstacles in their paths in different ways.

Elephants, bison, musk-oxen, sheep, and many deer moved comparatively easily from Asia to North America. On the other hand, the antelope Saiga tatarica and the yak could migrate no farther than Alaska (the obstacles beyond were insurmountable). The Rhinoceros tichorinus, musk deer, and squirrel were unable to overcome the obstacles in their paths.

Recently obtained data on the history of the Bering land mass and on the time at which it existed and was covered by a glacier (Saidova, 1961; Hopkins, 1959; Flint and Brantner, 1961) compel us to assume that this land bridge, serving as a path for a broad exchange of fauna repeatedly appeared and disappeared in the Cenozoic. During the Pleistocene it appeared in the form of slightly rolling, broad plains, permitting the migration of numerous mammals from Asia to North America (Flerov and Zablotski, 1961). It is therefore clear that the majority of species were able to migrate across this bridge, with the exception of those dwelling under specifically mountainous conditions as, for example, the musk deer (Moschus) which, a comparatively long time previously (probably in the second half of the Pliocene) had begun to inhabit mountains and a cold climate and had migrated to the north, although its ancestors had lived in warm, damp, forest regions. It was for this reason that it did not reach Kamchatka, which was separated by a strip of plain from its chief habitats. On the other hand it may be assumed that the Rocky Mountain goat (Oreamnos), an animal of undoubted Asiatic origin, had ancestors capable of crossing the plains when they migrated to America and that this goat itself changed only very recently into a true alpine form (at the beginning of the Pleistocene). The absence of the shaggy rhinoceros (Coelodonta antiquitatis) in Kamchatka and Alaska is also explained by landscape factors. The obstacles to the migration of this latter animal should be sought in the absence of suitable forage and in the cold climate prevailing at the time that a land bridge existed between Asia and North America.

It is an interesting fact that the bulk of the "migrants" moved from Asia to America and only a very few from America to Asia. Furthermore, these "Americans" penetrated for only a very short distance, keeping to Northeastern Asia. Only the caribou occupied broad stretches of the northern halves of Asia and Europe. It is evident that this phenomenon must be explained by the presence in Asia of abundant, varied biological mammal types occupying basic ecological niches.

In speaking of the migration of whole faunas, as mentioned above, it should be established that it is not the entire fauna which moves, but rather individual biocenotically and mutually related complexes of organisms. Certain species of a complex, however, find it easy to occupy new territories and to adapt to new conditions. Other species move more slowly and must

radically reorganize their ecology and morphology.

When there is little change in physicogeographical conditions, forms which have lived for a long time in the regions of their origin change little and slowly. That portion of a population which, in migrating, moves into conditions different from those prevailing in the region where the given form originated, frequently begins to change swiftly, adapting to the new conditions. In this case, morphological lability, the ability of organisms to change and adapt quickly, is the deciding factor enabling them to migrate and to occupy broad territories. In other words, the greater the ease with which an organism adapts to various conditions, the greater are its chances for increasing its geographical range.

In this respect eurybiontic forms above all have considerable advantages. Stenobiontic forms are fairly clearly divided into two groups. Among the first should be classed those species having sharply defined specific morphological adaptations permitting them to occupy only very narrowly limited ecological conditions. Upon entering other conditions, these species inevitably die, since they are deprived of the opportunity of acquiring the adaptations which they lost or are not capable of rapidly developing completely new structures. Long-necked giraffes, extinct sea cows and many others belong in this category. The second group should include forms adapted to life under strictly limited conditions but without sharply expressed specific morphological adaptations.

Thus various obstacles, which may be conventionally divided into orographical, ecological and morphological, have been of basic importance to the migration of terrestrial animals both in the present and in the past. The presence of ecological analogues replacing the forms and populations of organisms occupying a certain territory has also been of great importance. Thus, for example, numerous forms of Antilocapridae - complete analogues of the deer of Europe and Asia, occupying on these continents, biotopes corresponding to those of deer - were widely distributed in North America throughout the Miocene and much of the Pliocene. Deer began to develop and migrate rapidly upon the extinction in the second half of the Pliocene of the majority of genera and species of Antilocapridae in America (Flerov, 1950).

An inquiry into orographical and landscape obstacles requires investigation of the morphology of past fauna components and distribution factors; i.e., temperature, moisture, light, substrate, and so on. Answers to these questions call for a joint effort on the part of the paleozoologist, the paleobotanist, the lithologist and the paleogeographer. Only a many-sided investigation is capable of demonstrating the distribution of past organisms, biogeographical division into districts, and movements of and changes in fauna in the course of time.

More than a century of paleontological investigation has accumulated considerable material on the makeup and distribution of the animal and vegetable worlds of past geological ages. It was only in the 1920's, however, that there began a truly systematic study of the distribution of the mammals of the past in space and time. One of the first

attempts at such an investigation was G. Osborn's book Age of Mammals, published in 1910. A vast amount of material was later obtained by large expeditions in Europe, Asia, South Africa and South America. Prior to this the only past faunas of which we had anything approaching a complete knowledge were those of Europe, North and, partly, South America, North Africa (Al Fayyum) and Northern India (the Siwalik Range). At the present time, we have an idea of the basic faunistic complexes of almost all the continents, their makeup, the extent to which they changed in the course of time, and their distribution and migration. Hence it has become possible roughly to trace the past distribution of mammals, to analyse, in part, the main causes of changes in their distribution and to outline certain regular patterns observed in the history of mammal distribution. It is nonetheless imperative to continue the accumulation of faunistic material, to carry out excavations, etc., for, in general, our information is still very meager and here we are confronted with the widest possible field of activity. It is only in this way that we will come anywhere near ascertaining the taxonomy, morphology and phylogeny of extinct mammals and thereby study the adaptations, ecology and distribution of animals which formerly populated the earth. At the same time, ecological and biogeographical investigations represent one of the first and basic stages in studying the history of the earth. Paleobiogeography, then, in one of its aspects is included among those branches of knowledge which are concerned with the general problems of physical and historical geography.

Paleozoologists are confronted with important problems in addition to those outlined above. We have still not applied many new methods: radiation and bio- and geochemical techniques which, at their present level of development, can yield immense and extremely important theoretical and practical results, have still not been brought to bear on the problems of absolute age and paleoclimate. We are in very poor contact with special embryological studies which, as they now stand, have in certain cases yielded excellent results in the investigation of phylogeny. Our contacts with paleobotany are also unsatisfactory. There can be no doubt that our chief and immediate concern will be to organize this type of work. Therein lies the future of paleontology and paleobiogeography and the means by which they can advance to the front rank of biological sciences, bringing all of our research to a higher level.

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